

CONTINUITY AND CONTRAST IN MIDDLE AND LATE MIOCENE VERTEBRATE COMMUNITIES FROM THE NORTHERN TERRITORY.

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ABSTRACT

Comparisons of the the late Miocene Alcoota Local Fauna and the middle Miocene Bullock Creek Local Fauna reveal fundamental similarities in faunal composition and in the structure of the terrestrial component of their respective communities. The Bullock Creek palaeocommunity contains an abundance of aquatic and stream-bank species. Few aquatic species are present in the Alcoota palaeocommunity. The taxonomic succession is predominantly at the level of generic rank. The temporal succession by closely related ecomorphic species suggests continued integrity of the basic community structure. The Alcoota LF expresses an increase in species diversity and an increase in the body sizes of diprotodontids and macropodids that occurred during the approximately three million year long interval between the two local faunas. Biological, taphonomic and geological data indicate that both communities were intermittently subject to environmental stresses due to periods of low precipitation and high evaporation. The Bullock Creek Local Fauna shows evidence of seasonal aridity. The Alcoota Local Fauna shows evidence of one or more event-based mass mortalities due to regional drought.

KEYWORDS: Alcoota Local Fauna, Bullock Creek Local Fauna, Miocene, palaeocommunities, taphonomy, palaeoenvironment, succession.

INTRODUCTION

Since 1983, the Northern Territory Museum has been collecting vertebrate fossil material from the Alcoota Locality (22°52'S, 134°27'E), Alcoota Station, central Australia and the Bullock Creek Locality (17°7'S, 131°31'E), Camfield Station, northern Australia. Although certain Alcoota and Bullock Creek Local Fauna taxa have been widely compared on a systematic basis with related forms from other Australian Tertiary localities (e.g. Archer and Rich 1982, Murray and Megirian 1990), there have been no serious attempts to compare the whole faunas in terms of community structure, taphonomy, succession or inferred palaeoenvironments.

By way of a progress report we compare the species composition and taphonomy of the middle Miocene Bullock Creek Local Fauna (LF)

with those of the late Miocene Alcoota LF. The comparison is designed to examine the pattern of succession, the factors of mortality, the similarities and differences in community structure, the shared and contrasting palaeoenvironmental factors and the implications of the results in relation to other Australian Neogene local faunas. A brief and selective summary of the palaeontology of both localities is presented below.

Camfield locality. Fossils were discovered in the Camfield Beds at Bullock Creek by the Bureau of Mineral Resources (BMR) geologist C.G. Gatehouse in 1966 (Randal and Brown 1967, Plane and Gatehouse 1968). M.D. Plane of the BMR and associates undertook the first systematic collection, preparation and study of the Bullock Creek Local Fauna. Primary palaeontological publications resulting from BMR activities at Bullock Creek include Clemens and

Plane (1974), Rich (1979), Flannery *et al.* (1982), Smith and Plane (1985) and Murray *et al.* (1987).

Although other palaeontological parties visited the Bullock Creek fossil localities from time to time, further systematic collection recommenced with a survey by T.H. Rich (Museum of Victoria: NMV) and P.F. Murray (Northern Territory Museum: NTM), in 1983. Substantial collections of Bullock Creek material are now lodged with the BMR, NTM and NMV. The preliminary interpretations of the Bullock Creek Local Fauna presented here are based primarily on the NTM collection.

The Camfield Beds, which contain the Bullock Creek Local Fauna, consist of light coloured calcareous sandstone, siltstone and limestone with ferruginous mottling at the base and chalcidonic silification at the top (Plane and Gatehouse 1968) (Fig. 1). The most comprehensive account of the geology of the Camfield Beds is that of Randal and Brown (1967). The stratigraphy of the formation, based on a composite section measured by Randal and Brown (1967) along Bullock Creek, is shown in Figure 2.

Randal and Brown (1967:49) give the following interpretation of the environment of deposition: "The presence of algae and stromatolites indicate the sediments were deposited in shallow water. A near-shore environment is supported by fragmentation of fossil material, the conglomeratic material in the sequence, and the topographic situation of the unit. Deposition may have been in waters normally saline as indicated by the gypsum and barytes, but subject to freshwater flooding which brought in the gastropods. The environment may have been lacustrine, or associated with lagoons or estuaries frequently flooded by freshwater."

Because no marine animals are preserved in the Camfield Beds, (nor has any other organic evidence for a marine influence been identified), we interpret the presence of evaporites and lithoclastic carbonate deposits to be of non-marine origin and therefore indicative of periods of relatively dry, perhaps semi-arid, climatic conditions in the region (Megirian 1992). The inference of freshwater sedimentation producing the Camfield limestones is further supported by the abundant fish fauna which includes obli-

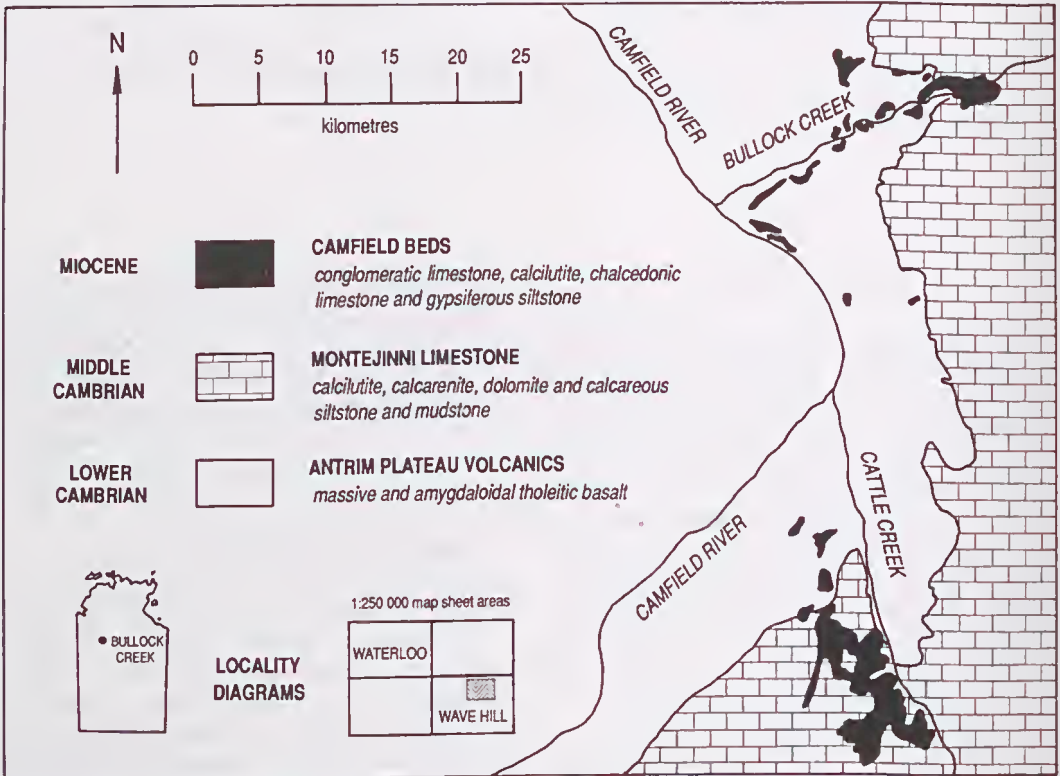


Fig. 1. Simplified geology of the Bullock Creek region showing the relationship of the Camfield Beds to basement formations and Recent drainage (after Bultitude 1973). Sweet *et al.* (1971) and Sweet (1973) identified a massive limestone cropping out in the southeastern part of the Waterloo map sheet area as Camfield Beds. No fossils are known to occur in these outcrops.

gate freshwater forms (eg. saratogas), all of which are relatively small-sized. Judging from the size of the remains, the largest teleost had a body-length of perhaps 20cm, and the largest lungfish is estimated to have been about 80cm body-length (A. Kemp, written communication). The palaeoenvironmental significance of the small size of the fish is explained below.

The NTM material was quarried from two distinct lithologies: conglomeratic limestone (Blast Site, Pebble Site, Far Site, Dromornithid Mountain, Top Site) and massive calcilutite (Site X and Site Y), interpreted to represent stream-channel and lacustrine facies respectively (Fig. 3). Siliceous pebbles and cobbles in the conglomeratic limestone are typically well-rounded, as are the limestone clasts. Some clasts in the Blast Site are composed of chalcedonic limestone in which fossil gastropods are preserved. These clasts are presumably derived from ancient weathered surfaces, suggesting that the Camfield Beds are diachronous, though no clear biostratigraphic evidence for this is available. Fragmented fossils in the conglomerates are typically sharp-edged and have not been transported far, though a few well-rounded bone fragments are also present. The latter may be reworked, indurated specimens of older age. The lithostratigraphic relationship of the quarried units is unclear; Site X and Site Y are probably within the same bed. The Blast Site is topographically low in the fossiliferous sequence (Fig. 3), but its stratigraphic relationship to other fossiliferous units is not known.

Much less material has been processed so far from the lacustrine sediments than from the conglomeratic sediments and the sample sizes are not comparable. However, there does not appear to be any significant taxonomic difference between the samples from the different lithologies, though the relative proportions of taxa vary. With the possible exception of the casuariid species, all taxa known from the calcilutites are represented in the Blast Site. The two facies appear to differ in that the calcilutites are particularly rich in fish and aquatic animals, and proportionally poor in terrestrial animals. The distribution of crocodylian taxa is compatible with this observation. The crocodyline *Harpacochampsia* Megirian, Murray and Willis, 1991, (a specialist piscivore) was found in lacustrine sediments in which *Baru* Willis, Murray and Megirian, 1990, appears to be rare, whereas in the Blast Site, *Harpacochampsia* is repre-

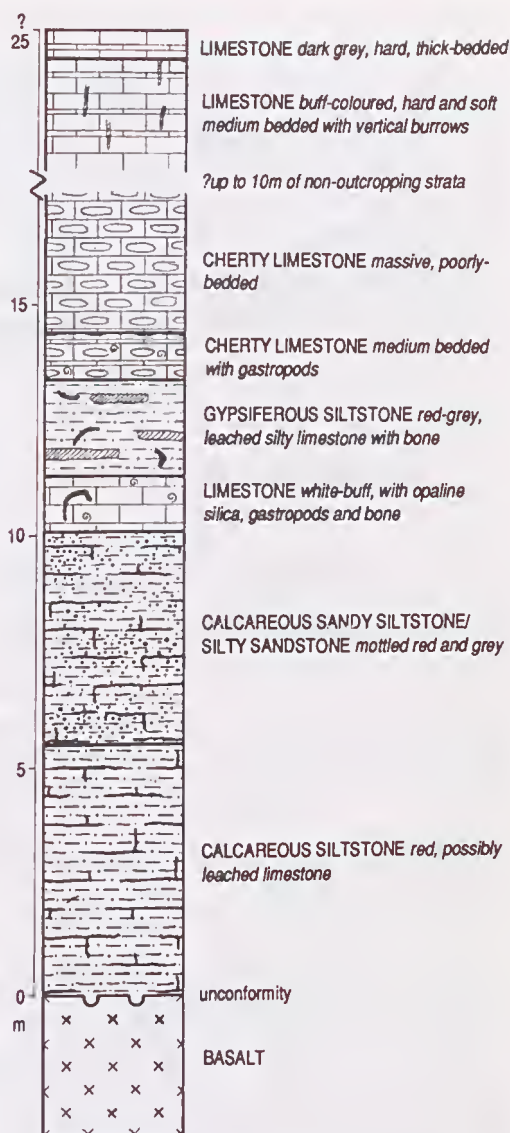


Fig. 2. Stratigraphic column of the Camfield Beds, based on a composite section measured along the Bullock Creek valley by Randal and Brown (1967:47).

sented by a single small individual found among numerous individuals of *Baru*. *Baru* was a stoutly-built, broad-snouted crocodyline with a massive dentition, and was interpreted by Willis *et al.* (1990) to be well adapted to quickly despatching large animals with its powerful bite. It may have inhabited shallow streams where dragging its prey into deep water was not an option. Excluding a few specimens of unrecorded provenance, all remains of a new species of *Quinkana* Molnar were collected at the Blast Site or from similar

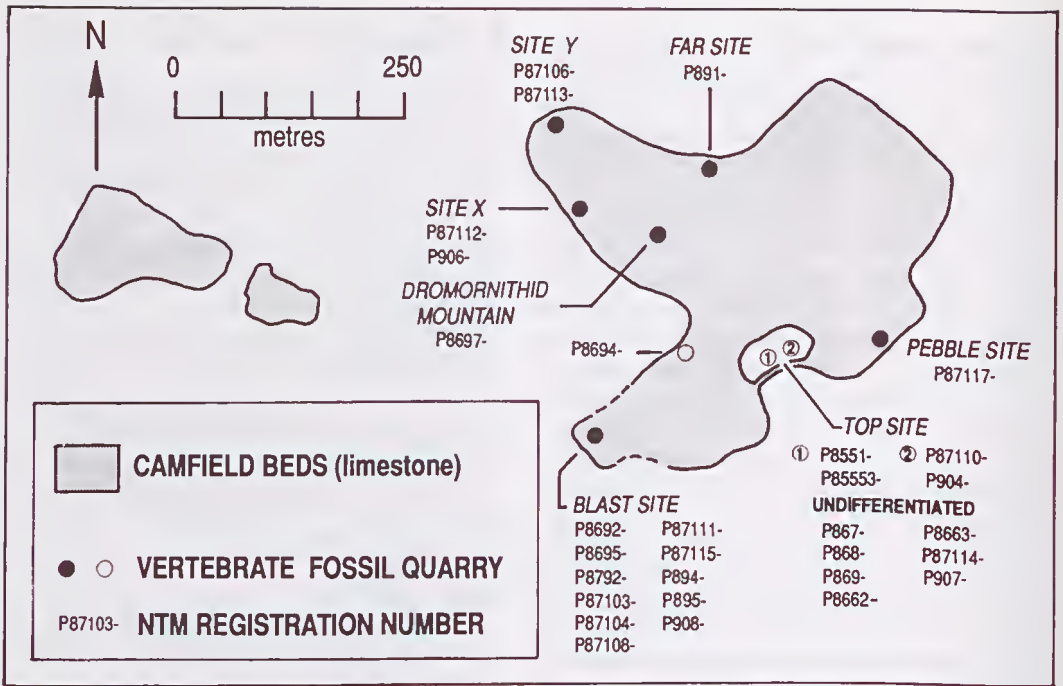


Fig. 3. Quarries worked by the Northern Territory Museum staff 1983-1989. Locality details are held on file at the Northern Territory Museum. Collections of fossiliferous limestone are initially given a registration number identifying their source. After extraction, individual fossils are uniquely identified by a numerical suffix, for example, P87103-25 is a specimen from the 'Blast Site'.

sites (Megirian in prep.). *Quinkana* was possibly a terrestrial crocodilian.

The fossilized bones are composed of apatite (calcium phosphate) (Fig. 4) as determined by powder X-ray diffraction. The presentation of the fossils ranges from poorly-sorted fragmentary lags to associations of partial skeletons among which complete crania, with delicate structures intact, are preserved. The Bullock Creek Local Fauna contains the taxa listed in Table 1, most of which are depicted in Figure 5.

The inferred age of the Camfield Beds is based upon the stage of evolution of the diprotodontid species *Neolielos* sp. which has been considered to be more advanced than the Kutjamarpu LF *N. tirarensis* but more primitive than the Alcoota LF diprotodontid *Kolopsis torus* (Woodburne *et al.* 1985).

Clemens and Plane (1974) considered the Kutjamarpu thylacoleonid species *Wakaleo oldfieldi* Clemens and Plane to be more primitive than the Bullock Creek LF *Wakaleo vanderleueri*. Additional Bullock Creek *Wakaleo* material described by Murray and Megirian (1990) shows fewer differences from *W. oldfieldi* than previously thought, indicating that the age of the

Bullock Creek Local Fauna is much closer to that of the Middle Miocene Kutjamarpu LF than to that of the Alcoota LF.

Propalorchestes novaculacephalus from Riversleigh 'System B' is indistinguishable from the Bullock Creek specimens (Murray 1990a). We agree with Woodburne *et al.*'s (1985) placement of Bullock Creek LF within the middle Miocene, but suggest that it might be situated a bit closer to the Kutjamarpu LF in age (transitional Bairnsdalian-Mitchellian Stage).

Alcoota locality. Two distinct Local Faunas have been identified in the Waite Formation: the Alcoota LF and the Ongeva LF (Murray *et al.* in prep.) (Fig. 6). The latter is significant in terms of biochronological estimation of the age of the Alcoota LF. Newsome and Rochow (1964) were the first to describe vertebrate fossils from Alcoota Station. A comprehensive study of the palaeontology of the Alcoota LF and geology of the Waite Formation was published by Woodburne (1967). Subsequent to Woodburne's investigation, sporadic excavations of the locality were undertaken by M. Archer, P.V. Rich, T.H. Rich and N. Pledge (Rich *et al.* 1982, Archer and Rich 1982). In 1984, the Northern Territory Museum

commenced an annual excavation program, establishing a permanent field station at the locality (Fig. 7).

The main fossiliferous units of the Waite Formation, Alcoota Station, are located about 350m apart. The lower lacustrine beds yielding the Alcoota LF are composed of unconsolidated, greenish-grey, silty sandstone with calcareous

partings and reddish-brown mottling. Evaporitic clasts, powdery carbonate residues and calcareous rinds are often associated with the fossil material. Patchy, tabular limestone bands occur sporadically above and below the fossil bed. Some limestone fragments have fine striations on their surfaces that resemble plant fossils (Woodburne 1967). These limestones differ from

Table 1. Bullock Creek Local Fauna. With the exception of Stirton, 1967, the unbracketed citations are both the authors of the taxon and the primary reference to the occurrence of that taxon at Bullock Creek. Bracketed citations are purely references to the occurrence of the taxon at Bullock Creek, and therefore should not be taken as an indication of a revision of the taxonomic concept.

MOLLUSCA	Gastropoda	(undetermined)
	Pelecypoda	(undetermined)
ARTHROPODA	Crustacea	ostracodes (undetermined)
PISCES (H.Larson pers. comm.)	Ceratodidae	(Lungfish) <i>Neoceratodus</i> (three species: Kcmp 1991)
	Osteoglossidae	(Saratoga)
	Ariidae	(Fork-tailed catfish)
	Plotosidae	(Eel-tailed catfish)
	Centropomidae	(Barramundi)
	Tetraodontidae	(Grunters)
AMPHIBIA (M. Tyler, written comm.)	Anura	<i>Australobatrachus</i> sp. <i>Litoria</i> spp.
REPTILIA	Pythonidae	gen. et. sp. indet. (Smith and Plane 1985)
	Madtsoiidae	<i>Yurlunggur camfieldensis</i> Scanlon, 1992
	Elapidae (Scanlon, written comm.)	(undetermined)
	Varanidae	<i>Varanus</i> spp. ? <i>Megalania</i> sp. (giant varanid)
	Meiolaniidae	<i>Meiolania</i> sp. nov. Megirian, in press (Megirian 1989)
	Chelidae	(undetermined)
AVES	Crocodylidae	<i>Barn darrowi</i> Willis, Murray and Megirian 1990 <i>Harpacochompsa camfieldensis</i> Megirian, Murray and Willis 1991 <i>Quinkana</i> sp. nov. (Megirian in prep.)
	Dromornithidae	<i>Bullockornis planei</i> Rich 1979 <i>Bullockornis</i> sp.. (Rich 1979) <i>Dromornis</i> sp.
	Casuariidae	<i>Dromaius</i> sp. (Patterson and Rich 1987:87) (undetermined)
	Anatidae	(undetermined) Other undetermined non-ratites
MAMMALIA	Dasyuridae	(undetermined)
	Thylacinidae	<i>Nimbacinus dicksoni</i> Muirhead and Archer, 1990
	Peramelemorphia	"V.D." bandicoots (Muirhead pers.comm.)
	Thylacoleonidae	<i>Wakaleo vanderleueri</i> Clemens and Plane, 1974
	Diprotodontidae	<i>Neohelos</i> cf. <i>tirarensis</i> Stirton, 1967 Gen. et sp. nov ("Nimbador") <i>Propalorchestes novaculacephalus</i> Murray, 1986
	Palorchestidae	(undetermined)
	Phalangeridae	(undetermined)
	Pseudocheiridae	(undetermined)
	Potoroidae	(undetermined)
	Macropodidae	<i>Balbaroo camfieldensis</i> Flannery, Archer and Plane, 1982 <i>?Nambaroo</i> sp. (H. Godthelp and M. Archer written comm.) large kangaroo (?Sthenurinae) small kangaroo (high-crowned tooth) Other species of small, undetermined marsupials
	Chiroptera	(undetermined microchiropteran)

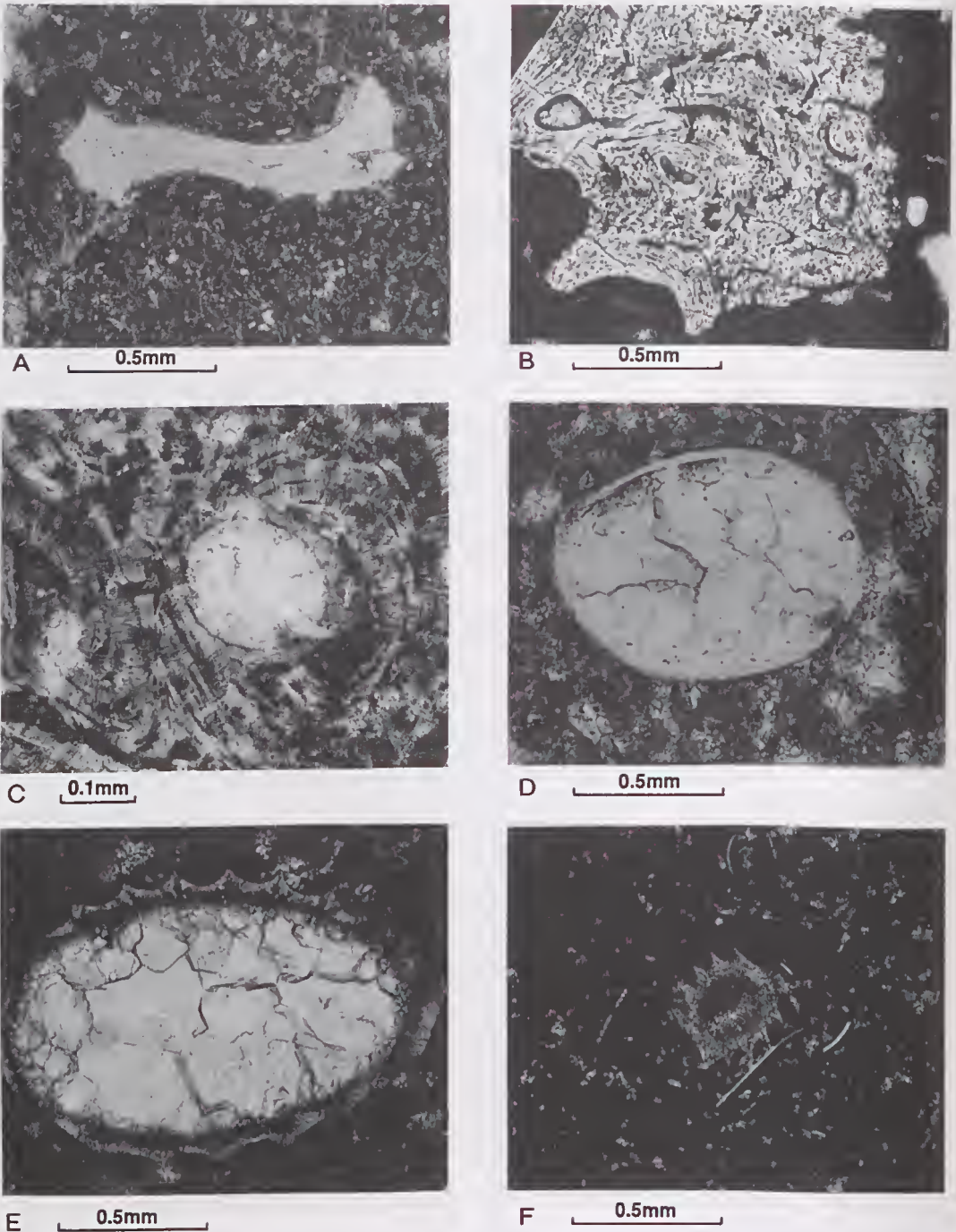


Fig. 4. Photomicrographs of thin sections of Camfield Beds limestone. **A**, probable fish bone in micritic matrix. Powder X-ray diffraction indicates the fossil bones are composed of calcium phosphate (apatite). The characteristic black colour of many Bullock Creek fossils is due to iron and magnesium oxides deposited within the bone, revealing internal structure clearly; (**B,C**) detail of Haversian system; **D**, articulated ostracode valves in transverse section; **E, F**, oogonia of charophyte algae. All primary voids are filled with sparry calcite cement. All plane polarized light.

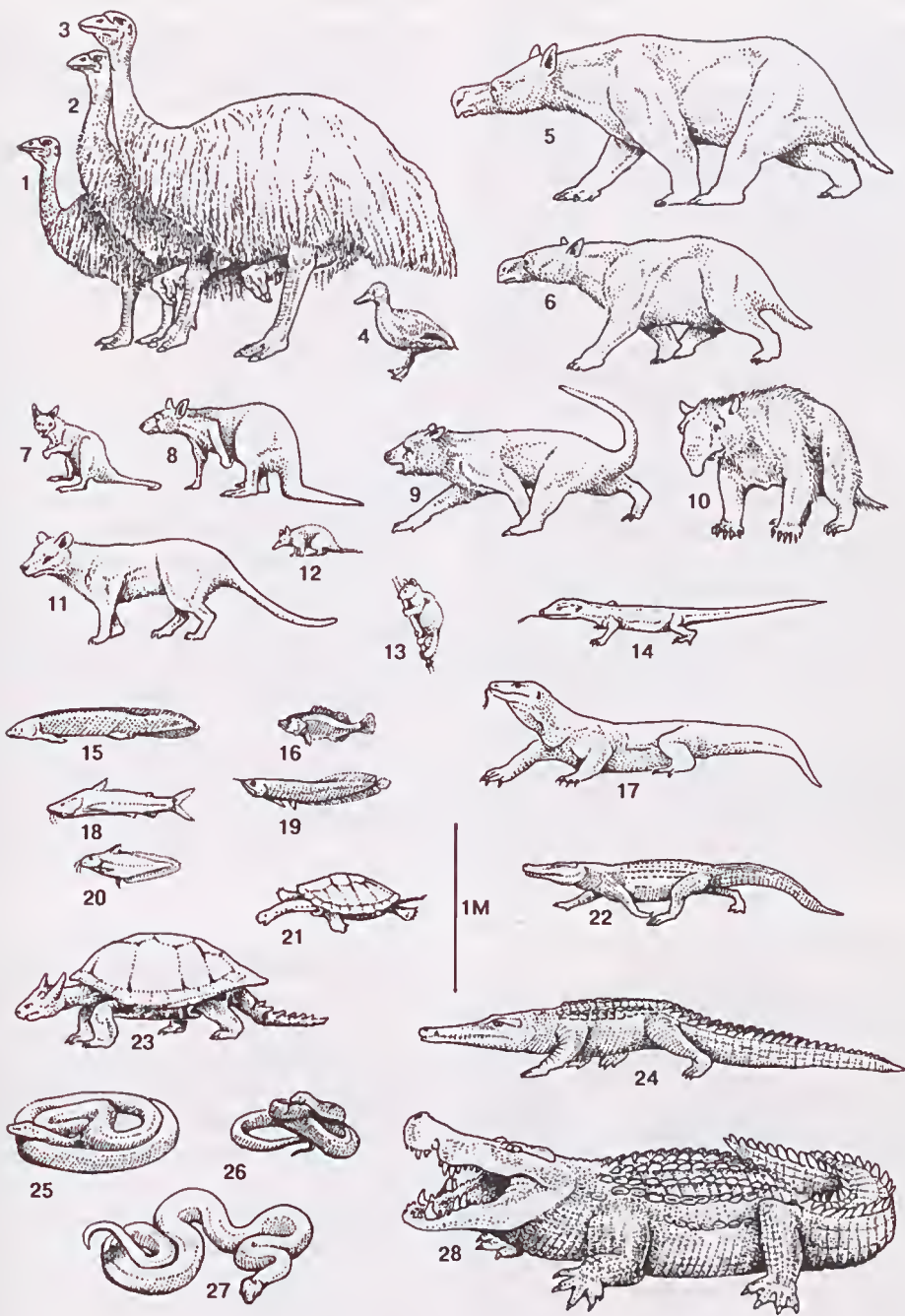


Fig. 5. Reconstructions of mid Miocene Bullock Creek Local Fauna, drawn approximately to scale; 1, casuariid; 2, dromornithid, *Bullockornis* spp. (one of two species); 3, *Dromornis* sp.; 4, Anatidae (undetermined duck); 5, *Neohelos* cf. *tirarensis*; 6, small zygomaturine diprotodontid "*Nimbadon*" (Hand *et al.*, unpublished); 7, Macropodidae (undetermined species with high-crowned molars); 8, Balbarinae (one of two species); 9, thylacoleonid *Wakaleo vanderleueri*; 10, palorchestid *Propalorchestes novaculacephalus*; 11, small thylacinid, *Nimbacinus dicksoni*; 12, Peramelamorphia ("VD" bandicoot); 13, one of three species of generically undetermined phalangeroids; 14, Varanidae, (undetermined, larger than *Varanus giganteus* (perentie), ?immature cf. *Megalania*); 15, Ceratodontidae (undetermined lungfish, cf. *Neoceratodus*); 16, Centropomidae (one of several undetermined perch-like fishes); 17, large varanid, *Megalania*-sized; 18, Ariidae (forktailed catfish); 19, Osteoglossidae (Saratoga); 20, Plotosidae (Eel-tailed catfish); 21, emydid turtle (genus undetermined); 22, crocodylid, *Quinkana* sp. nov.; 23, meiolaniid, *Meiolania* sp. nov.; 24, crocodylid, *Harpacochampsia camfieldensis*; 25, pythonid (genus undetermined); 26, elapid, (genus undetermined); 27, madtsoiid, *Yurlinggur camfieldensis*; 28, crocodylid, *Baru darrowi*.

the chalcedonic limestone caprock of pedogenic origin and may represent spring-related carbonate deposits or travertines.

The fossils sometimes occur as isolated, associated partial skeletons, but are more often concentrated in a bone bed or in poorly defined channel deposits encountered between 0.50m and 0.90m below the ground surface (Fig. 8). The condition of the material ranges from very complete crania with fragile structures intact to very fragmented, and totally dissociated, specimens concentrated together in an extensive, tangled mass of bones. Large, well-preserved specimens often occur in association with dissociated fragmentary concentrations of bone where the former have acted as snags.

The distribution and condition of the fossil material indicates very localized transport of the smaller bones and fragments, accompanied by rapid sedimentation. The partial association of the remains of large animals suggests a moderate degree of predepositional scattering, which appears to have taken place at the surface during and after decomposition. The bone bed has the

sedimentological attributes of short-interval, high-energy hydraulic transport similar to that which occurs in arid to semi-arid basins at present as a result of runoff from infrequent, but prodigious, downpours.

The fossilized bone of the Alcoota Local Fauna is distinctive in being extensively crazed by alternate expansion and contraction of the clay fraction of the matrix, due to fluctuations in the moisture content of the siltstone over millions of years. A curious product of this agency is the gradual expansion of structures by the incorporation of fines into the cracks as the matrix swells, gradually "exploding" some of the bones and teeth. Some burial compaction and distortion of the fossils seems to have occurred, but other causes of compaction and crushing are discussed below. Our analysis of the chemical composition of the fossil bone and its matrix is incomplete. Powder X-ray diffraction reveals that the primary component of the fossilized bone is calcium phosphate (apatite). The Alcoota Local Fauna contains the taxa listed Table 2, most of which are depicted in Figure 9.

Table 2. The Alcoota Local Fauna. Unbracketed citations are both the authors of the taxon and the primary reference of the occurrence of the taxon in the Alcoota LF. Bracketed citations are purely references to the occurrence of the taxon at Alcoota, and do not imply a revised taxonomic concept.

MOLLUSCA	Gastropoda	(undetermined)
REPTILIA	Testudines	Emydidae
	Crocodylidae	<i>Baru</i> cf. <i>darrowi</i>
	Varanidae	? <i>Megalania</i>
AVES	Casuariidae (undetermined)	<i>Dromaius</i> sp. (Patterson and Rich, 1987)
	Dromornithidae	<i>Dromornis stirtoni</i> Rich, 1979
		<i>Ilbandornis lawsoni</i> Rich, 1979
		<i>Ilbandornis woodburnei</i> Rich, 1979
	Anatidae	(undetermined ducks)
	Aecipiteridae	(undetermined hawks and eagles)
Phoenicopteridae	(undetermined flamingo)	
MAMMALIA	?Peramelemorphia	(undetermined)
	?Dasyuridae	(undetermined)
	Thylacinidae	<i>Thylacinus potens</i> Woodburne, 1967
	Thylacoleonidae	<i>Wakaleo alcootaensis</i> Archer and Rich, 1982
	(Vombatidae)*	(undetermined)
	Diprotodontidae	<i>Pyramios alcootense</i> Woodburne, 1967
		<i>Alkwertatherium webbi</i> Murray, 1990b
		<i>Plaisiodon centralis</i> Woodburne, 1967
		<i>Kolopsis torus</i> Woodburne, 1967
	Palorchestidae	<i>Palorchestes pamei</i> Woodburne, 1967
	Petauridae	<i>Pseudochirops</i> sp.
	Maeropodidae	<i>Hadronomas puckeridgei</i> Woodburne, 1967
		<i>Dorcopsoides fossilis</i> Woodburne, 1967
cf. <i>Dorcopsoides</i> (<i>Protemnodon</i>)*		

*The vombatid and the *protemnodon* kangaroo were reported by Woodburne (1967) as tentative identifications. We have not found any remains assignable to these groups during our investigations.

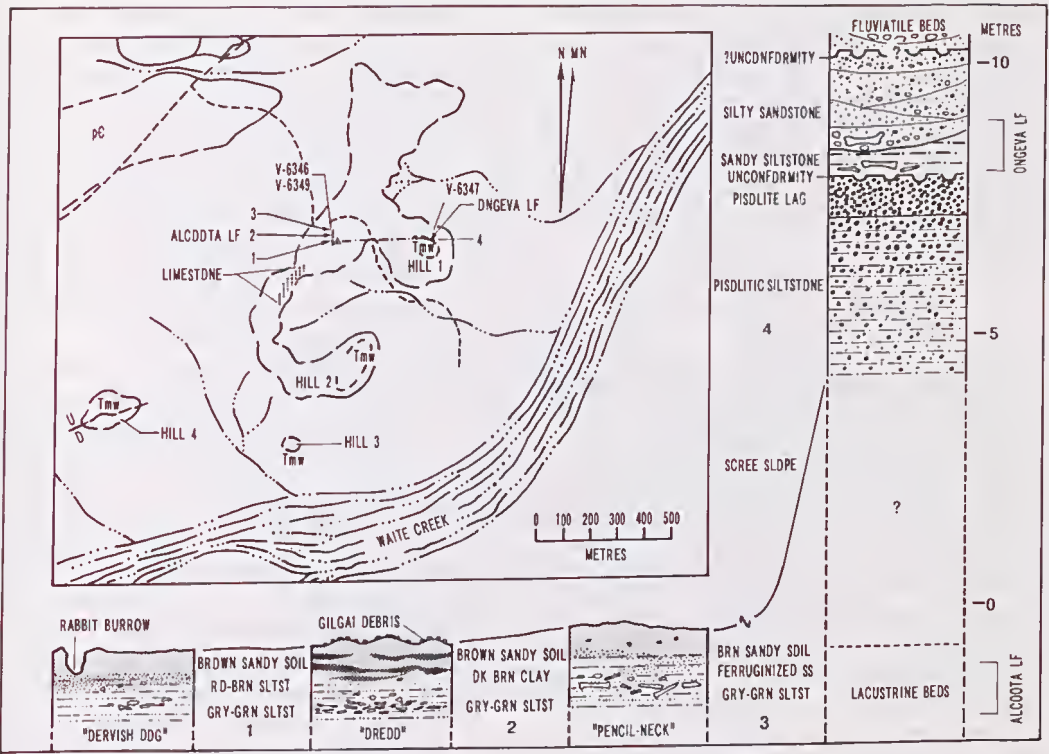


Fig. 6. Map and representative sections of Alcoota fossil localities; numbers correspond to sample sections from each of three main Alcoota Local Fauna quarries shown in Fig. 7. Geological map based on Woodburne (1967: Fig. 2); V-numbers correspond to Woodburne's University of California Museum of Paleontology locality designations. The stratigraphic section on the right shows the relationship of the Ongeva Local Fauna (not described in this paper) to the Alcoota Local Fauna. *Kolopsis* sp. nov. from the Ongeva Local Fauna constrains the age of the Alcoota LF more precisely than was previously possible (Murray *et al.* in prep.).

The age of the Alcoota Local Fauna was considered post-Kutajmarpu LF, pre-Beaumaris LF in age by Stirton *et al.* (1967) on the basis of the stage of evolution of the diprotodontid fauna. Woodburne *et al.* (1985:359) cast some doubt on the pre-Beaumaris age of Alcoota with the statement "The above discussion of problems concerning the material referred to *Zygomaturus gilli* (Beaumaris) raises the possibility that the Alcoota sample may have existed contemporaneously with or even later than, the Beaumaris Local Fauna". The recent discovery of a more derived *Kolopsis* species, similar to the Beaumaris form, in a fluvialite stratum of Hill 1, situated unconformably 6.8m above the Alcoota LF (Fig. 7), provides a strong indication that the lacustrine beds are significantly older than Beaumaris (Murray *et al.* in prep.). Consequently we suggest that the Alcoota Local Fauna is transitional Mitchellian-Cheltenhamian Stage equivalent (Late Miocene).

METHODS AND MATERIALS

Representative samples of fossil material from the Alcoota and Bullock Creek localities were analysed using the proximity method outlined by Shotwell (1955). Shotwell's descriptive statistical approach seems ideally suited to the faunal assemblages from Alcoota and Bullock Creek in which many postcranial elements are represented. The entire samples of Alcoota and Bullock Creek material, estimated to be of the order of three or four thousand specimens, have not yet been fully analysed. Furthermore, some sample collections of material sent to colleagues several years ago have not yet been identified or returned. Consequently, the assignments of smaller species are given at higher taxonomic levels, and accurate quantification of some forms, e.g. fishes, has not been possible.

We have assembled two samples of material that we can confidently identify at the level

indicated. Shotwell's method is not intended to test or assess the statistical significance of sample differences, but to elucidate patterns in faunal assemblages that would otherwise be extremely laborious or awkward to express verbally. Inevitably, because of the ongoing nature of our project, the quantitative details of the present analysis will be superseded as new material is acquired.

RESULTS

Systematic affinities. Although the Alcoota and Bullock Creek Local Faunas share no mammalian species and only a few mammalian and reptilian genera (Fig. 10), there is substantial evidence of systematic continuity in the majority of taxa. *Wakaleo alcootaensis* appears to be derived from *W. vanderleueri* (Murray and Megirian 1990). The postulated diprotodontid succession *Neohelos tirarensis* to *Kolopsis torus* is structurally of the order of a species-rank differentiation, but its principal distinction, the division of the paracone and metacone on P³, is a quintessential synapomorphy uniting *Kolopsis* with the more derived *Zygomaturus* clade (Stirton *et al.* 1967).

The genus *Plasiodon* may share an ancestor with *Neohelos* (Stirton *et al.* 1967). There are no features of *Propalorchestes novaculacephalus* that would preclude its ancestry to *Palorchestes painei* (Murray 1990a). Specific antecedents to the Alcoota zygomaturine *Alkwertatherium webbi* or the diprotodontine *Pyramios alcootense* have not been found in the Bullock Creek assemblage. Primitive nototherines, structurally suitable as ancestors to *Pyramios*, are known in early to mid Miocene sediments at Riversleigh, Queensland (Archer *et al.* 1989).

Macropodid phylogeny in mid to late Miocene Local Faunas is also poorly documented. *Balbaroo* and *Nambaroo* both share a few dental and anatomical features with *Hadronomas* (Murray 1991). A sthenurine-like femur from Bullock Creek could represent a *Hadronomas* annectant. The small undetermined wallabies from Bullock Creek could represent early members of the *Dorcopsoides* clade. *Niubacinus*, a thylacinid genus from Bullock Creek, possesses no features that would preclude its ancestry to *Thylacinus* (Muirhead and Archer 1990).

The three Alcoota dromornithid species may be descendants of a large undetermined Bullock Creek species. Rich (1979) considered *Bullockornis* a sister genus to *Dromornis*. Of these, only *Dromornis* is a structurally suitable ancestor for *Ibandornis*. The Alcoota casuariid, an unnamed species with features structurally intermediate to the emu and cassowary, differs from the Camfield form primarily on the basis of its slightly larger size.

Preliminary work on the Alcoota crocodylids indicates the presence of the genus *Baru*. The Alcoota *Baru* species closely resembles *Baru darrowi* from the Bullock Creek LF but may represent a chronospecies. Systematic evidence suggests that the majority (about 85 per cent) of mammalian and avian genera and species in the Alcoota Local Fauna could have been derived from Bullock Creek species during the intervening three million years.

Sampling Variation. Comparison of the NTM Alcoota collection with Woodburne's (1967) published inventory provides an example of the statistical variation in the sampling (Fig. 11). The proportions of species in the NTM samples vary from year to year, but the combined 1984-1990 samples have resulted in proportions similar to those calculated from data in Woodburne (1967). The primary differences are registered in our lower frequencies of *Pyramios alcootense* and

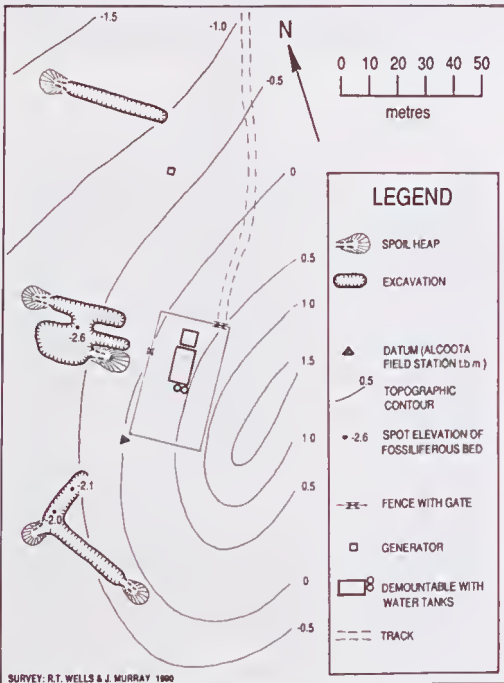


Fig. 7. Plan of Alcoota Local Fauna fossil quarries and NTM field station.

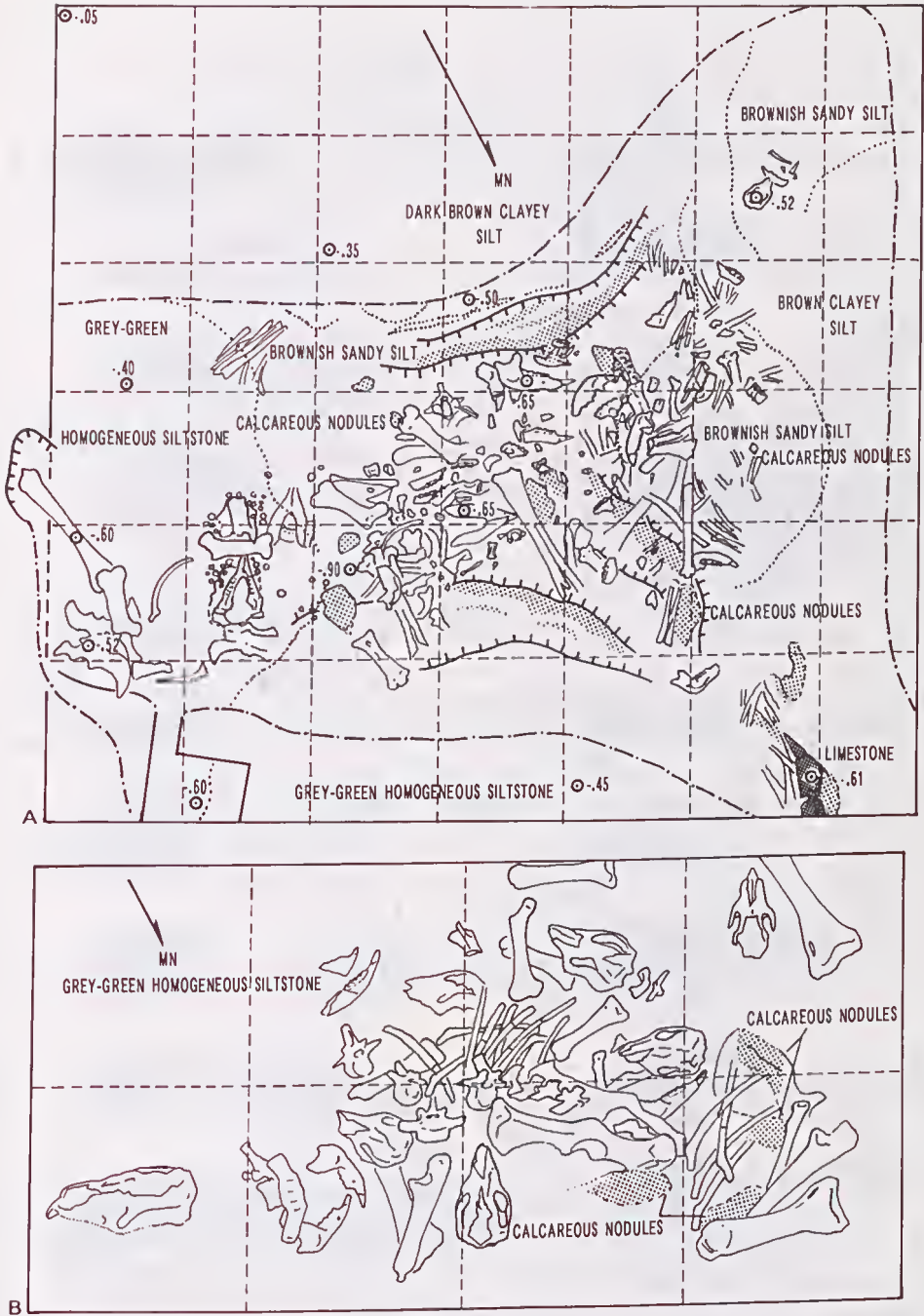


Fig. 8. Two types of assemblages at Alcoota: A, channel deposit containing dense mixture of fragmented specimens; about one-third of them have been depicted here (field sketch 3-7-88 to 5-7-88); B, associated remains of a single large diprotodontid (*Plaisiodon centralis*) acting as a trap for smaller remains, in this case six crania, partial posterianal remains and several dentaries of *Kolopsis torus* (field sketch, 23-8-87). Spot elevations were determined with line-level from the south corner of the excavation; stipple represents a localised concentration of soft, powdery and ehalky, or crystalline minerals thought to represent evaporites, together with diagenetic calcaireous nodules. The left lower quadrant of A shows a concentration of gastroliths in association with dromornithid sternum and synsaeum fragments. In B, the large cranium to the left is *Plaisiodon*, which is considered to represent the species of the larger associated diprotodontid remains. The *Plaisiodon* specimen and one of the more complete *Kolopsis torus* skeletons from this assemblage are on display as armatured partial restorations in the Spencer and Gillen Museum, Alice Springs.



Fig. 9. Reconstructions of the late Miocene Alcoota Local Fauna, drawn approximately to scale; 1, anatid (undetermined duck); 2-3, smaller accipiterids, at least two species; 4, phoenicopterid, undetermined flamingo; 5, zygomaturine diprotodontid, *Plaisiodon centralis*; 6, casuariid, 7, dromornithid, *Ibandornis woodburnei*; 8, *Ibandornis lawsoni*; 9, *Dromornis stirtoni*; 10, zygomaturine diprotodontid, *Alkwertatherium webbi*; 11, zygomaturine diprotodontid, *Kolopsis torus*; 12, diprotodontine diprotodontid *Pyramio alcootense*; 13, palorchestid, *Palorchestes painei*; 14, macropodid, *Protomnodon* (Woodburne 1967); 15, large accipiterid, possibly an eagle; 16, perameloid (undetermined genus); 17, thylacoleonid, *Wakaleo alcootaensis*; 18, macropodoid, *Dorcopsooides fossilis*; 19, macropodid, *Hadronomas puckridgi*; 20, dasyurid (undetermined); 21, ?vombatid (Woodburne, 1967); 22, emydid (undetermined genus); 23, petaurid, *Pseudocheirops* sp.; 24, macropodid (undetermined genus); 25, varanid. cf. *Megalania*; 26, thylacinid, *Thylacinus potens*; 27, crocodylid *Baru* cf. *darrowi*.

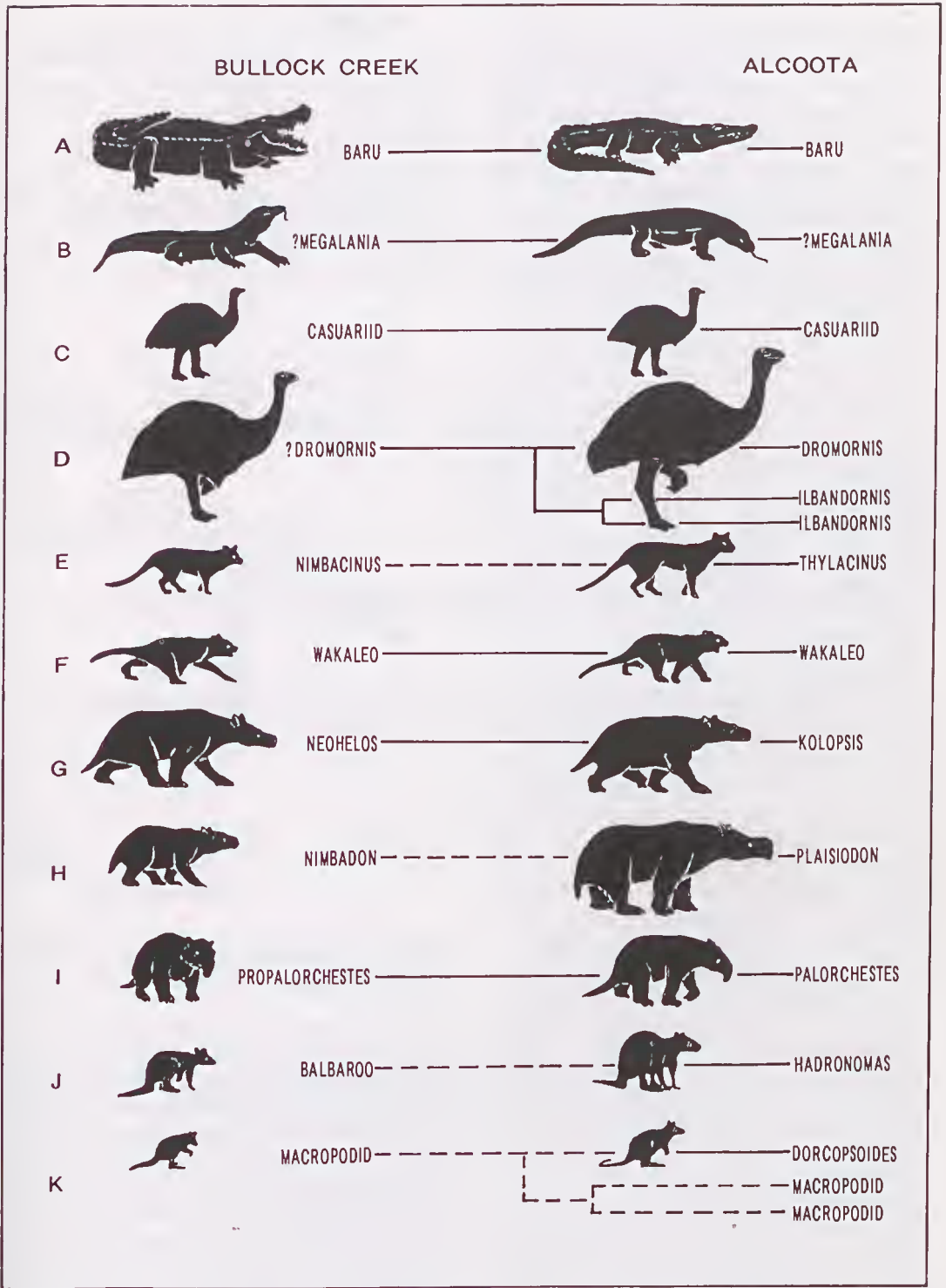


Fig. 10. Hypothesis of ecological succession of closely related, ecomorphically similar species; A, *Baru darrowi*-*Baru* cf. *darrowi*; B, *?Megalania* sp.-*Megalania* sp.; C, casuariid - casuariid; D, *?Dromornis* sp.-*Dromornis stirtoni*; E, *Nimbacinus dicksoni*-*Thylacinus potens*; F, *Wakaleo vanderleueri*-*Wakaleo alcootaeusis*; G, *Neohelos* cf. *tirarensis*-*Kolopsis torus*; H, "*Nimbadon*"-*Plaisiodon centralis*; I, *Propalorchestes novaculacephalus*-*Palorchestes painei*; J, *Balbaroo camfieldensis*-*Hadronomas puckeridgei*; K, macropodid-*Dorcopsoides fossilis*.

Palorchestes painei, complemented by a higher frequency of *Dorcopsoides fossilis* (plus a similar but larger unidentified macropodid species) and *Kolopsis torus*. At present there is no comparable control for the NTM Bullock Creek Local Fauna sample, but the potential exists for eventual comparison of the NMV collection made by T. Rich and associates.

Community structure. According to the model of Shotwell (1955), taxa showing a large number of specimens per individual and a high relative abundance may, *in general*, be considered members of the community in closest proximity to the depositional environment ('proximal community'). The obvious corollary is that taxa represented by few specimens per individual at a low relative abundance probably belong to a distant community. Clearly there are a large number of uncontrolled variables that can influence the relative abundance of a species and the estimated number of specimens per individual. In the following interpretation we first draw attention to the similarity between the Bullock Creek and Alcoota Local Faunas, before accounting for the differences.

Comparison of the frequency distributions of Bullock Creek LF and Alcoota LF species-equivalents (i.e. shared ecomorphs) shows that in this category the two faunas are quite similar in relative abundance of species and in species diversity (Fig. 12). The most conspicuous contrast between the two assemblages is the large number of aquatic and stream-bank species in the Bullock Creek Local Fauna. Over half the identified species at Bullock Creek are fish, crocodiles, snakes, varanids and turtles. These groups account for less than one quarter of Alcoota species (Fig. 13), indicating that permanent aquatic-riparian habitats at Alcoota were remote from the depositional setting. Pythonids, pythonid-like madtsoiid snakes, and meiolaniid tortoises (all absent from Alcoota) are represented at Bullock Creek at a low relative abundance but by a high number of specimens per individual, and are thus considered to represent the proximal habitat at Bullock Creek.

Other differences in the faunas are the occurrence of two additional, though rare, diprotodontid species and a higher relative abundance of macropodids at Alcoota. Our interpretation of the Alcoota sample suggests that the diprotodontid genera *Pyramios* and *Alkwertiaherium* belong to a distant community. The Alcoota macropodid sample contains ap-

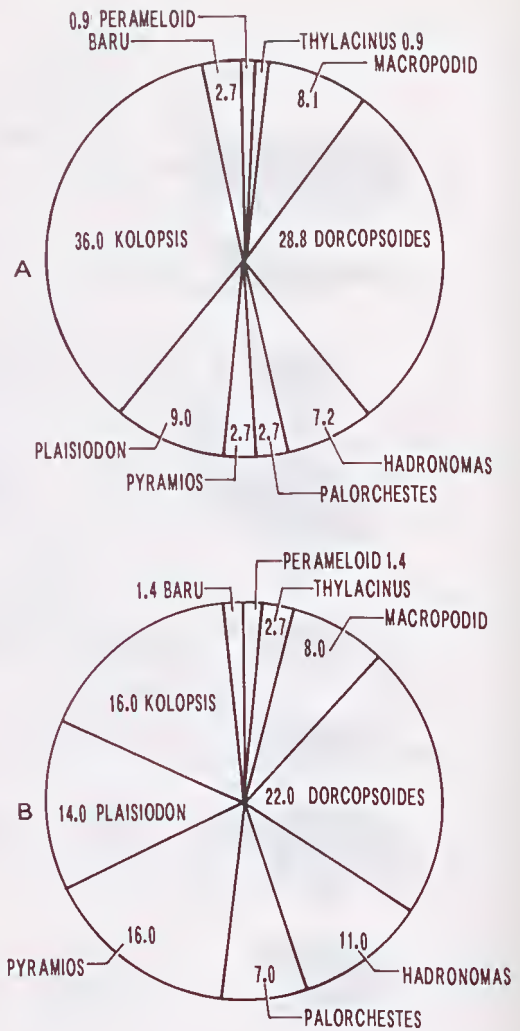


Fig. 11. Relative abundance of equivalent taxa collected from Alcoota by the NTM to 1980 (A) for comparison with Woodburne (1967) (B).

proximately four times as many individual kangaroos as the Bullock Creek LF, and on the average, they are represented by much larger species (Fig. 14). Because the number of specimens per individual for kangaroos does not differ greatly between the two assemblages, an ecofacies bias seems unlikely, hence kangaroos can be considered elements of the proximal community at both localities. The frequency difference is attributable to an increase in favourable kangaroo habitat in combination with a concomitant increase in kangaroo numbers at Alcoota. Although body size enlargement and morphological specialization is apparent in the Alcoota macropodid species, the diversity of genera re-

mains low in comparison to Plio-Pleistocene Local Faunas.

Secondary consumers such as mammalian carnivores are normally present in small numbers relative to the number of primary consumers. Thus, the carnivorous marsupials *Wakaleo* and *Thylacinus* are considered members of the proximal community at both localities. Browsing palorchestines are known from numerous Neogene assemblages, but are uncommon in all of them, including in the Alcoota and Bullock

Creek Local Faunas. Their low frequency in a wide variety of depositional settings might reflect solitary habits, and therefore we tentatively include palorchestines with the proximal community of both Alcoota and Bullock Creek.

Casuariids are rare and poorly represented in terms of specimens per individual, indicating that they are distant community species in both assemblages. Phalangeroids are uncommon at both localities, although the species diversity is higher at Bullock Creek (the sample includes

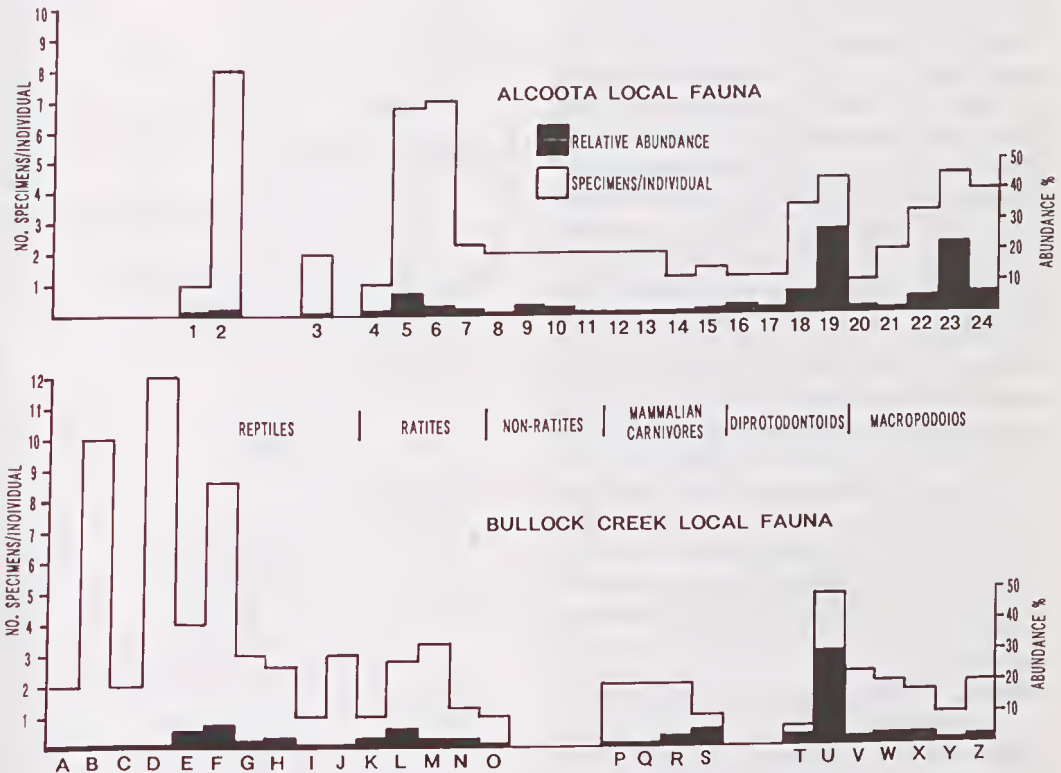


Fig. 12. Histogram comparing relative abundance of species (black columns) and estimated number of specimens per individual (white columns) from Alcoota and Bullock Creek faunal assemblages using the procedure originated by Shotwell (1955) and employing a standard number of elements of 50. Annectant and/or closely related ecomorphic species and genera are aligned. Numerical abbreviations (Alcoota): 1, emydid (undetermined); 2, *Baru* cf. *darrowi*; 3, large varanid (probably *Megalania*); 4, casuariid; 5, dromornithid *Dromornis stirtoni*; 6, *Ilbandornis woodburne*; 7, *Ilbandornis lawsoni*; 8, Anatidae (undetermined duck); 9, Accipiteridae (?two species); 10, Accipiteridae (?eagle); 11, Phoenicopteridae (undetermined Flamingo); 12, perameloid (undetermined genus); 13, dasyurid (undetermined); 14, thylacinid, *Thylacinus potens*; 15, thylacoleonid, *Wakaleo alcootaensis*; 16, diprotodontid, *Pyramios alcootense*; 17, diprotodontid, *Alkwertatherium webbi*; 18, diprotodontid, *Plaisiodon centralis*; 19, diprotodontid, *Kolopsis tornus*; 20, palorchestid, *Palorchestes painei*; 21, petaurid, *Pseudocheirops*; 22, macropodid, *Hadrononous puckeridgei*; 23, macropodid, *Dorcopsoides fossilis*; 24, macropodoids (undetermined). Alphabetical abbreviations (Bullock Creek): A, pythonid (undetermined); B, madtsoiid, *Yurlanguur camfieldensis*; C, elapid (undetermined); D, meiolaniid, *Meiolania* sp. nov.; E, emydid (undetermined); F, erocodylid, *Baru darrowi*; G, erocodylid, *Harpacochampsia camfieldensis*; H, erocodylid, *Quiukana* sp. nov.; I, large varanid (cf. *Megalania*); J, small varanid (undetermined); K, casuariid.; L, dromornithid, *Bullockornis* sp.; M, dromornithid, *Bullockornis planei*; N, dromornithid, ? *Dromornis* sp. O, Anatidae (undetermined duck); P, perameloid, ("VD" bandicoot); Q, dasyurid (undetermined); R, thylacinid, *Nimbacinus dicksoni*; S, thylacoleonid, *Wakaleo vanderveueri*; T, diprotodontid, "*Nimbodon*" gen. nov.; U, diprotodontid, *Neohelos* cf. *tirareus*; V, palorchestid, *Propalorchestes novaculacephalus*; W, phalangeroids (undetermined); X, Macropodidae, *Balbaroo camfieldensis*; Y, ?Balbarinae (undetermined); Z, macropodoids (undetermined).

three species represented by isolated teeth). Phalangeroids appear to be distant community representatives in both assemblages, from which relatively few other species of small mammals have been recovered.

The higher frequency of specimens per individual of large ratite birds (dromornithids) at Aleoota may be attributable to the greater massiveness of the elements which were less likely to be destroyed or dispersed by surface weathering and depositional agencies. The more active fluvial depositional environment at Bullock Creek may have resulted in greater dispersal of ratite elements.

Taking all species in each assemblage into account, the secondary consumer to primary consumer ratios based on categorical numbers are basically the same (Fig. 15 A,D). However, there are marked contrasts between Aleoota and Bullock Creek taxa when expressed in terms of relative abundance. (Fig. 15 B,E). At Aleoota, the carnivore guild is poorly represented in taxonomic diversity and in relative abundance. The mammalian predators in the Aleoota carnivore guild are somewhat larger than the Bullock Creek forms, which, when expressed in terms of estimated biomass, results in a slightly higher ratio of primary to secondary consumers (Fig. 15 C,F).

The poor representation of the carnivore guild at Aleoota and the apparently contrasting abundance of carnivores at Bullock Creek is probably not indicative of the typical predator-prey ratios in either of these communities. Explanation of the differences requires additional information from taphonomy and inferred habitat structures, as detailed below.

Palaeoenvironments. *Bullock Creek Locality.* The geology and biology of the Bullock Creek assemblage indicates a fluvio-laeustrine environment with permanent and at least seasonally-abundant water. The existence of seasonally shallow, ephemeral laeustrine, pond or oxbow slough habitats are denoted by the presence of numerous, uniformly small teleosts that had become trapped in the basins and died due to deoxygenation of the water or possibly as a result of total dessication. A slow-moving, relatively warm riverine environment is indicated by the presence of freshwater stromatolites.

A moderately large meandering river, subject to significant seasonal fluctuations in flow sufficient to produce oxbow sloughs, and a large flood plain accounts for the Bullock Creek bio-coenosis. The low frequency of phalangerids supports the inference that the local vegetation

was not arboreous. A typical active floodplain might be dominated by subclimax associations of sedges, possibly grasses and scrub. If a woodland or forest habitat was present at all, it was situated a considerable distance from the depositional environments. The fauna reflects a waterhole assemblage around which larger

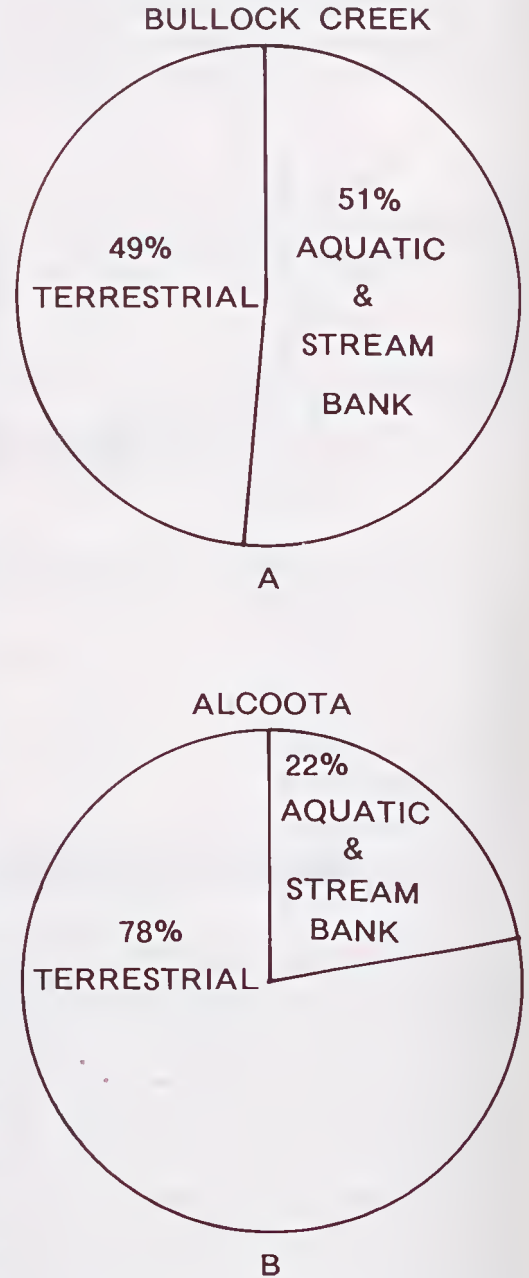


Fig. 13. Comparison of relative proportions (by number of individuals) of aquatic to non-aquatic fauna between A, Bullock Creek Local Fauna and B, Aleoota Local Fauna.

predators would be expected to congregate (Fig. 16A).

Two or more specific ecotopes are discernable among the several quarry samples from the

Camfield Beds limestone. The massive calcilutites at Sites X and Y, containing numerous fish remains and a piscivorous crocodylian, signify a relatively deep basin which may represent a reach of a sluggish river or a seasonally flooded oxbow slough, associated with nearby swamp and shallow ponds. The fossil material is dispersed throughout the sediment as though flushed out and held in suspension for a short distance away from its original source. The Blast Site, Top Site and Dromornithid Mountain Site may represent point bar accumulations or low energy fluvio-lacustrine deposits in which minimal transport and dissociation has occurred. Unfortunately, the samples from Sites X and Y are too small for quantitative comparison using the method proposed by Shotwell (1955).

During intermittent or seasonal droughts, large species such as *Neohelos* congregated near the water. Crocodile predation, for which there is evidence in the form of tooth punctures in bones, accounts for an as yet undetermined, but perhaps significant, proportion of the mortality of *Neohelos* and *Palorchestes*. We have not statistically analysed the mortality of *Neohelos* on the basis of tooth-wear estimates of age, but all age-categories are present, with very old specimens and very young specimens being rare. We consider our *Neohelos* sample to represent a normal (i.e. having typical mortality patterns) population structure.

The sedimentologically complex deposits at Bullock Creek indicate that the fossil accumulations are not confined to a single event or to a temporally-restricted series of events. The assemblage represents sequential accumulations, possibly punctuated by seasonality and local sedimentological conditions over some unknown, but perhaps geomorphologically significant, period of time (i.e. a period of time not resolvable by stage-of-evolution methods). The biological evidence supports the sedimentological evidence of the existence of relatively dry conditions over northern Australia during the Miocene (McGirian 1992).

Alcoota Locality. The Alcoota Locality represents an ephemeral fluvio-lacustrine environment with a very localized, possibly spring-fed, permanent water source. The sedimentology indicates that the deposit represents a shallow lacustrine basin subject to large fluctuations in water level. When full, the basin would have held a very shallow lake several kilometres in diameter (Fig. 16B). The low water level condition of the basin is indicated by partially articu-

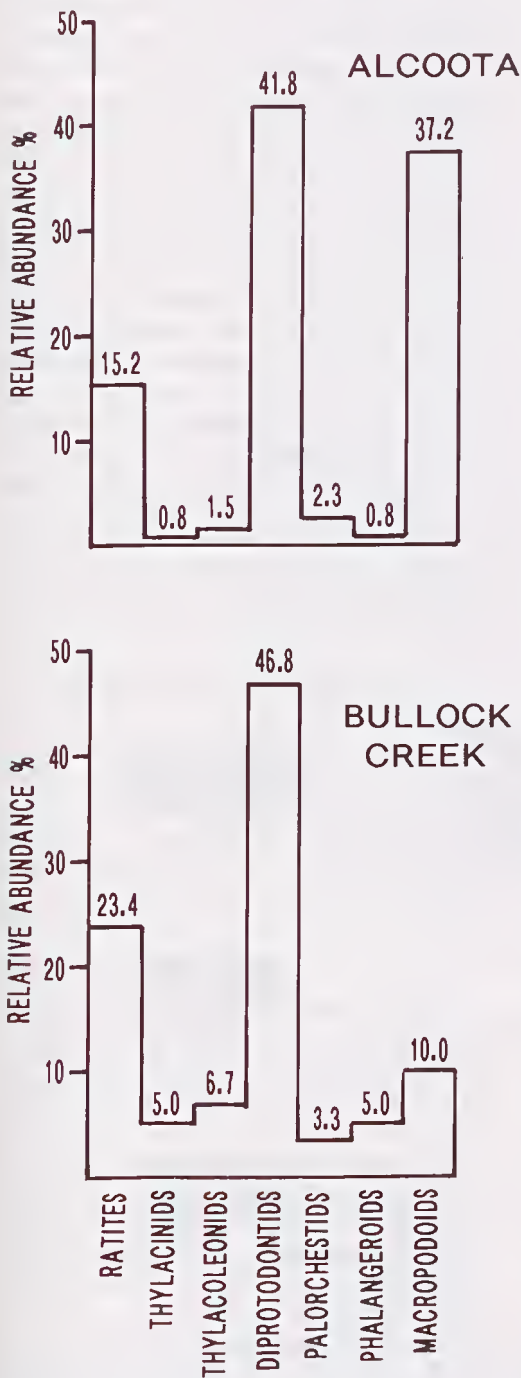


Fig. 14. Histograms comparing relative abundance of the predominant terrestrial taxa in the Alcoota and Bullock Creek Local Faunas.

lated skeletons being concentrated near what appears to be the centre of the basin. If these animals died locally, as opposed to having been transported, their presence is indicative of a dry basin. Even in the unlikely event that these associations represent bloated floating carcasses, a drastically reduced water level or relatively small lake or pond must still be postulated in order to account for the concentration.

An ephemeral lacustrine environment is also indicated by the extreme rarity of turtles and the absence of fish. Crocodiles, though well represented in terms of numbers of specimens, are not abundant in terms of numbers of individuals. The low relative abundance of crocodiles can be explained by their propensity to move overland or follow water courses to avoid being trapped and overcrowded in shrunken waterholes (Weigelt 1989). The large, localized accumulation of uniformly weathered fossils, in combination with the sedimentological evidence for rapid, short distance, and high sediment-yielding hydraulic transport, suggests that the Alcoota LF represents an event-controlled assemblage.

The taphonomic features of the Alcoota assemblage are very specific. There are more species of Diprotodontidae found together than

in any other described Local Fauna. The fossil material is highly localized and concentrated, uniform in pre-burial weathering, but varies widely in extent of fragmentation. The deposit is evidently synchronous and sedimentologically uniform. Partially articulated or associated large species are often devoid of their small elements such as phalanges. The large elements (diprotodontid skulls, innominates, femora) trap smaller elements and fragments transported from some short distance upstream. Members of the same species of larger animals are found in association with one another more often than expected if the distribution were random. Large dromornithid birds have been found in association with concentrations of gastroliths (Fig. 8A).

Uniform weathering of the material indicates that the assemblage was exposed at the surface long enough for complete soft-tissue decomposition and secondary scattering, but not sufficient to allow disintegration of the outer surface of the bone. Differential fragmentation of skeletons is partially explained by hydraulic transport, but some material was unevenly fragmented *in situ* due to crushing. If this crushing was entirely attributed to burial compaction, the damage should be locally uniform and all broken

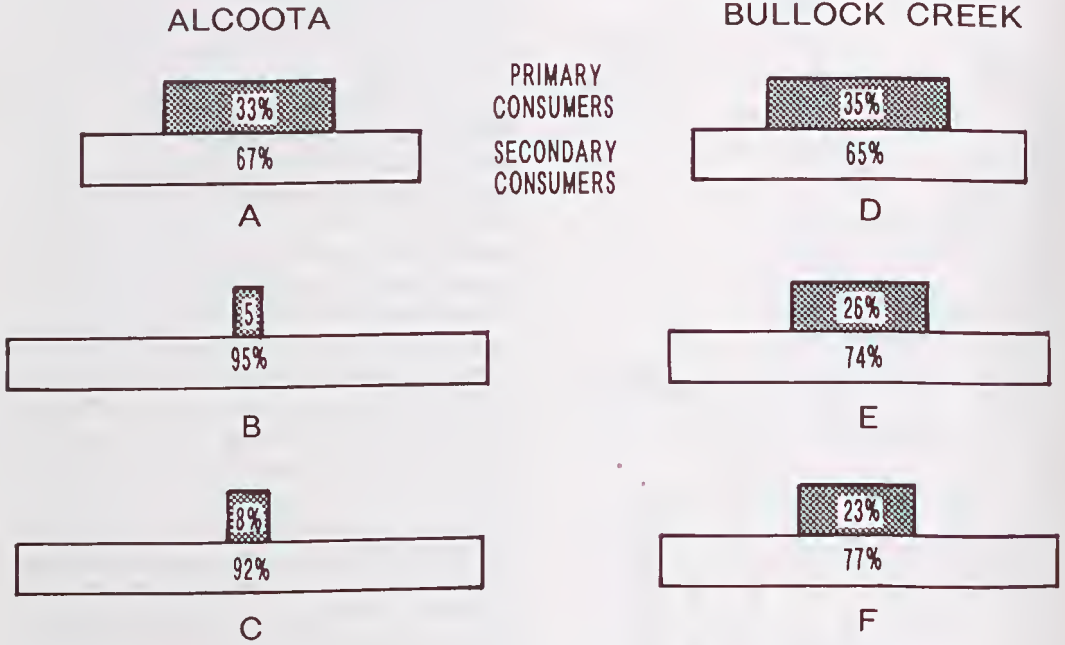


Fig. 15. Ratios of primary to secondary consumers in the Alcoota LF, A-C, with the Bullock Creek LF, D-E. Three types of comparison are made: A, D, (top) number of species, all taxa; B, E, (middle) relative abundance, each species; C, D, (bottom) relative abundance X estimated weight of each individual (biomass). Fish species have not been quantified and are therefore not included in the middle and lower graphs. Small mammalian carnivores (perameloids and dasyurids) are included with secondary consumers in the middle and lower graphs.

pieces would be present. However, there are specimens in the Alcoota assemblage that appear to have been crushed before burial, because some fragments produced by crushing are missing, presumably due to transport.

A possible cause of this type of damage could be trampling by large animals. There are also localized areas of dense compaction and flattening of elements in the bone bed. Animals of the same species are often found together, independent of their size, within very circumscribed areas. For example, the two *Hadronomas* crania occurred close together, while six *Kolopsis* crania, associated dentaries and postcranial elements were found in one small area (Fig. 8B). These observations suggest that the assemblage represents a mass mortality caused by 'waterhole tethering', a relatively common phenomenon that takes place during periods of prolonged drought (Weigelt 1989, Behrensmeyer and Boaz 1980). As ephemeral waterholes dry out, animals become concentrated around remaining permanent water sources, greatly increasing the biomass of the local community. As a result, the available forage is overconsumed, leaving the animals to die of starvation in the proximity of the waterhole.

Herding animals mill around the waterhole until they die, often in close proximity to one another. Survivors trample and pad over deceased animals, compacting and scattering their remains. Under extreme conditions, such animals normally associated with distinct and sometimes distant communities are congregated together, hence the exceptionally large number of diprotodontid species at the site. Eventually the majority of them die of starvation around the water hole; others wander off in search of food to eventually die of thirst.

The comparatively low number of carnivores at Alcoota is probably due to the local guild being overwhelmed by a rapid influx of large herbivores from other communities. There is no evidence of carnivore damage to the Alcoota material. Moreover, it is unlikely that carnivores would respond reproductively to a tethering event, or abandon their territories in the short term, in order to scavenge a distant concentration of carcasses (Behrensmeyer and Boaz 1980).

The remains of these tethered animals lay on the dry surface of the lake until they were incorporated into the sediments when the drought was broken by significant rainfall. Runoff from a single rainfall event would have been sufficient

to orient, scatter and bury the Alcoota assemblage exactly as palaeontologists have found it.

The Alcoota palaeoenvironment is considered to represent a subtropical savanna with local forest in the protected gullies of the Proterozoic hills surrounding the basin. The rarity of small, arboreal animals in the assemblage supports the inference that the proximal landscape was sparsely vegetated with possibly sedge, tussock grasses and subclimax scrub formations immediately around the lake shore, and savanna beyond, extending to the ranges. The thick, poorly-sorted sediment layer, resulting from fluvial activity associated with sporadic flooding suggests the presence of a considerable area of unvegetated or sparsely vegetated ground surface in the catchment (Schumm 1968). The biological and sedimentological evidence of periodically severe aridity indicates that the nearby presence of a closed canopy forest formation on the surrounding plain was unlikely.

CONCLUSIONS

The major conclusions are that the Bullock Creek and Alcoota Local Faunas demonstrate systematic and community structural continuity from the mid to the late Miocene in northern Australia. The Camfield Beds (yielding the Bullock Creek LF) assemblage contains biological evidence of seasonality (trapping of small fish in drying backwaters), while lithostratigraphic evidence (interbedded evaporites) suggests longer periods of low precipitation and probably high ambient temperatures.

The Waite Formation at Alcoota contains biological and taphonomic evidence of stress (temporarily unbalanced predator-prey ratio; indications of event-based mortality; massive, uniformly weathered fossil accumulations) and geological evidence of periodic aridity (presence of evaporites; evidence of fluctuating water table; evidence of rapid erosion and deposition of texturally-immature sediments, suggesting locally-poor vegetation cover). Both palaeocommunities have small mammal species as a background element, and the dearth of arboreal forms indicates an absence (locally) of closed canopy or evergreen rainforest.

Our palaeoenvironmental reconstruction of the Bullock Creek mid Miocene (Bullock Creek LF time) habitat is that of a meandering river on a wide floodplain, with oxbow lake and

streambank communities predominating. Local fringing forest may have been present on stable outer oxbow margins and on the erosive bank of meanders. Successional plant formations such as sedges and subclimax scrub, grading to woodland, may have been present on the accumulative margins (Fig. 16A). The precipitation regime oscillated from subhumid to semi-arid on an annual basis. Interbedded evaporites in the Camfield Beds indicate periods of aridity during the mid Miocene, reflecting longer term climatic variability.

The Alcoota Locality appears to have represented a small but permanent, possibly spring-fed pond or lake, sometimes expanding to a temporary, large, shallow lake. A wide margin of sedge or grassland, grading to woodland and gully forest, surrounded the outer margin of the basin (Fig. 16B). The region was subject to periodically severe drought, resulting in tethered congregations of large mammals and event-controlled mortality. The precipitation regime oscillated between subhumid and semi-arid, but was apparently less reliable than at Bullock

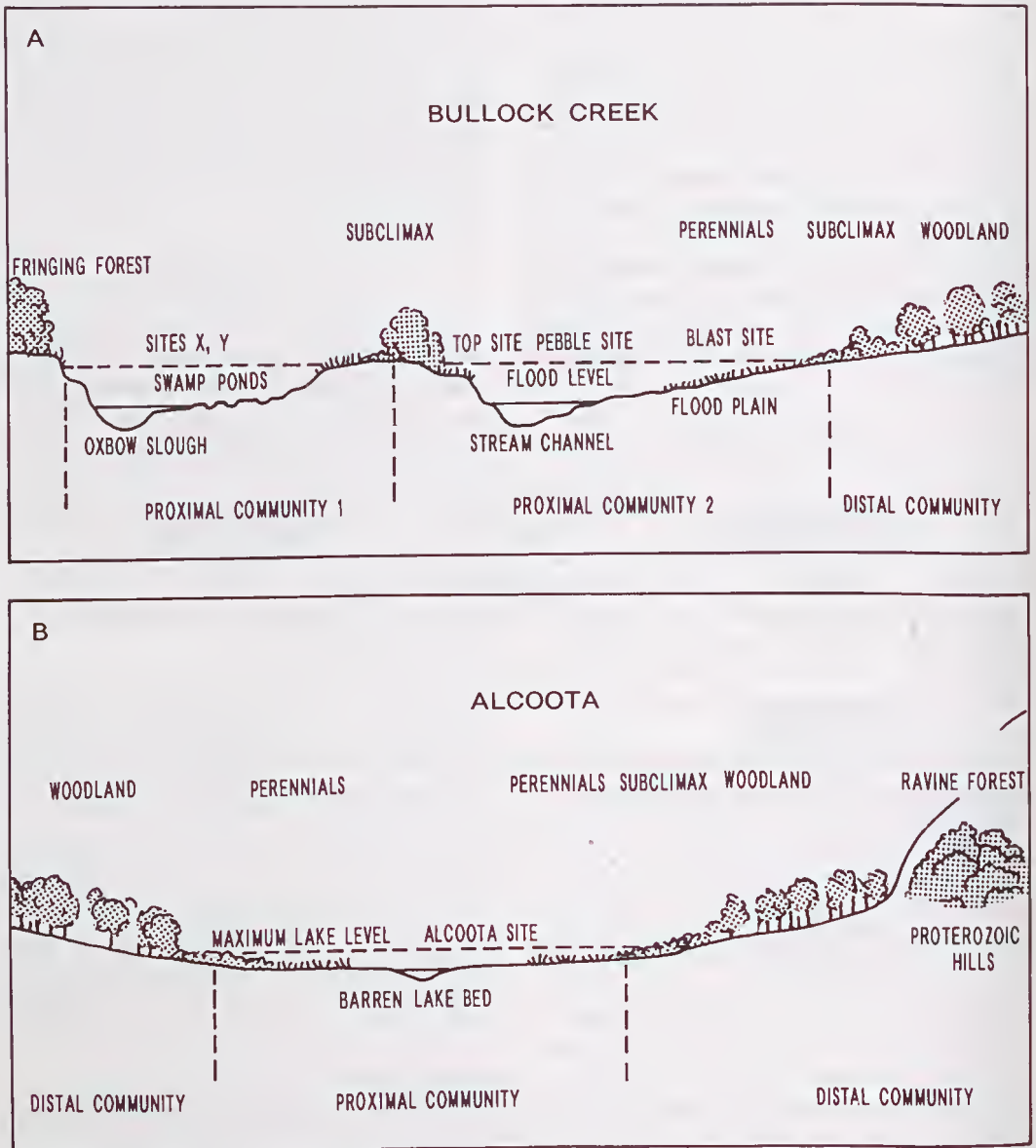


Fig. 16. Schematic reconstruction of palaeohabitats at A, Bullock Creek and B, Alcoota, (vertically exaggerated).

Creek during the times represented by limestone deposition (i.e. Bullock Creek LF time).

These hypotheses convey several implications for Australian Neogene community evolution and biogeography. Principal among them is evidence from mid and late Miocene fossil assemblages that aridification and concomitant habitat diversification was in progress in northern Australia during the mid Miocene and had probably commenced much earlier. Supporting evidence comes from the palaeobotanical record (Kemp 1978, Lange 1983, Truswell and Harris 1982, Nix 1982, Hill 1992) which suggests that aridity was already a feature of central Australia in Eocene times. The concept of a pan-Australian closed canopy rainforest persisting into the mid to late Tertiary from the Paleocene is not supported in any of these investigations.

The extant plant formations of northern Australia are neither venerable remnants of ancient widespread rainforests, nor geologically young communities established since the continent reached its present position in relation to Sundaland. They are unique communities that have gradually evolved in response to the tectonic movement of the continent northward, and to a lesser extent in relation to increased biogeographic influences from Southeastern Asia (Webb *et al.* 1986, Truswell *et al.* 1987). Similarly, Australia's arid-adapted flora, now covering much of the interior of the continent, has an equally long evolutionary history (Truswell and Harris 1982, Nix 1982). Consequently, there are no model plant communities or existing analogous plant communities to which we can refer that would specifically characterize the formations inferred for the Miocene of northern and central Australia.

However, it is possible to characterize the structural aspect of these communities. The geological evidence for significant fluctuations in precipitation combined with tropical or subtropical temperature regimes is very substantial. The local vegetational patterns of both the Alcoota and Bullock Creek localities must have been heavily dominated by flood plain successions, resulting in a significant corridor of un-forested habitat around the depocentres. Fluctuations in the precipitation regime of the magnitude suggested by our observations would not support a predominantly closed canopy forest, but might support local rain green formations and woodland or tree savanna. The possibility of the existence of extensive savanna-like communities in northern Australia during the mid to late

Miocene should not be ruled out, as the conditions appear to have already been suitable for such structures.

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